POPULATION FLUIDITY IN *LEPTOTHORAX LONGISPINOSUS* (HYMENOPTERA:FORMICIDAE)*

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Introduction

Although social insect colonies are commonly conceived as stable entities in time and in space, considerable information exists to demonstrate that population fluidity can be pronounced. Data on ants show that workers can be exchanged between nests (Kannowski 1959; Scherba 1965; Chauvin and Leconte 1965; Alloway *et al* 1982; Del Rio Pesado and Alloway 1983; MacKay and MacKay 1983); a colony can undergo budding (Scherba 1958; Talbot 1961; Brian 1965; Cherix *et al* 1980; Stuart 1985; Pamilo *et al.* 1985); and entire nests can move from one site to another (Van Pelt 1976; Smallwood and Culver 1979; Smallwood 1982; Droual 1984; Herbers 1985). These observations lead to the conclusion that in some species the colony is not a fixed entity, but rather a shifting collection influenced by ecological contingencies.

That a given colony can occupy more than one physical nest site, a condition known as polydomy, deserves particular attention (Fletcher and Ross 1985). Evolutionary dynamics under conditions of colony fractionation are poorly understood, even though the consequences for eusocial evolution may be profound. There is surprisingly little information to document and measure the extent of population fluidity for any species, a gap we help to fill in this paper.

Recent work demonstrates that some species of leptothoracine ants are polydomous (Alloway *et al* 1982; Del Rio Pesado and Alloway 1983; Stuart 1985). These inconspicuous temperate species are well-suited for detailed studies of polydomy because they are small and easy to culture. Here we quantify nest fission, fusion, migration, and other features of polydomy for *Leptothorax longispinosus* kept under semi-natural conditions in the laboratory. While

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a complete understanding of population fluidity must be predicated on work conducted in the field, our results provide insight into the evolutionary ecology of this ant.

Population structure in *L. longispinosus*

Many ants of the genus *Leptothorax* are polygynous (Buschinger 1968, 1974), and *L. longispinosus* is no exception (Talbot 1957; Headley 1943; Alloway *et al* 1982). Previous work on the E. N. Huyck Preserve (Albany County, New York) showed the population to be facultatively polygynous: some nests contain no queen, others have one, and still others have multiple queens (Herbers 1984). Moreover, there was a strong winter-summer dichotomy in queen distribution. Many nests in summer are queenless, whereas in winter such groups are rare (Herbers 1986a); similarly, the average number of queens per nest is lower in summer. Finally, nests are considerably more spread out in summer than in winter (Herbers 1985). These results are best explained as correlates of a seasonal shift in spatial structure: colony fractionation in summer and condensation for overwintering. It appears that, for the most part, overwintering nests are independent colonies that become polydomous in summer when they fractionate to occupy several nest sites (Herbers 1986a). This cyclic polydomy hypothesis is supported by behavioral evidence reported below.

Methods

Nests of *L. longispinosus* were excavated from the New York site in late October 1983, when they exhibited spatial relationships and a distribution of queens among nests that is typical of winter. Each nest was returned to the laboratory and removed from its stick, acorn, or root. The ants were then resettled into glass tubes 10 cm long and 4 mm in diameter. Each nest was put into a separate box and incubated at 4° C for overwintering. In March the temperature and light-dark cycles were slowly incremented to match outside conditions. On May 8, 1984 the conditions were stabilized at 14 hours of light. On that date, we positioned 17 nests on 4 artificial forest floors to duplicate their spatial positions in nature the previous fall (Figure 1). Observations and censuses were then conducted until August 27, 1984, when the experiments were terminated.

The artificial forest floors were 1m × 1m in size. Each had a red glass base upon which autoclaved pine needles, leaf fragments and other debris typical of the habitat were scattered. The sides of the floor were coated with petroleum jelly to prevent worker escapes, and the entire structure was enclosed in mosquito netting to restrict alate fights. Lights above and below the red glass base provided illumination. The temperature was maintained at 18–20° C and relative humidity at 60–90%. Periodically water was sprinkled on the floor to simulate rainfall. In addition to placing nests on the floor according to where they had been collected, we supplied additional tubes so that each floor had a total of 10 nesting sites. Nests were supplied with water *ad libidum* and solid food (both frozen fruitflies and a formula based on Bhatkar and Whitcomb's (1970) recipe) three times weekly. Detailed observations of behavior were taken for the first 3 weeks (2 hours of continuous observation daily from 9:00–11:00 as well as periodic checks), after which the intensity of observation was reduced to 2 hours per week. Nests were censused daily for the first two weeks and weekly for the rest of the period.

Results

The initial contents of nests are given in Table 1. Four nests on 1A (all polygynous), three nests on 1B (one queenless, one monogynous, one polygynous) and five nests on 2B (two queenless, one monogynous, two polygynous) were positioned to duplicate their natural locations with respect to each another (Figure 1).

Direct observations of the ants showed that initially aggression was common: workers engaged in fighting behavior, wherein two workers would interlock mandibles, attempt to sting each other, push or pull by the mouthparts, and so on. These encounters sometimes resulted in death of one or both participants. Not all interactions were aggressive, however; workers were observed to carry other workers, brood, and in one case a queen outside the nest. Several occasions of tandem running (which usually precedes a colony migration (Möglich 1978) were observed. In addition to interacting with other ants, workers were often observed to explore, forage, and manipulate pieces of detritus and food.

Particularly striking was exploration of the empty tubes which represented potential new nesting sites. This exploratory behavior is

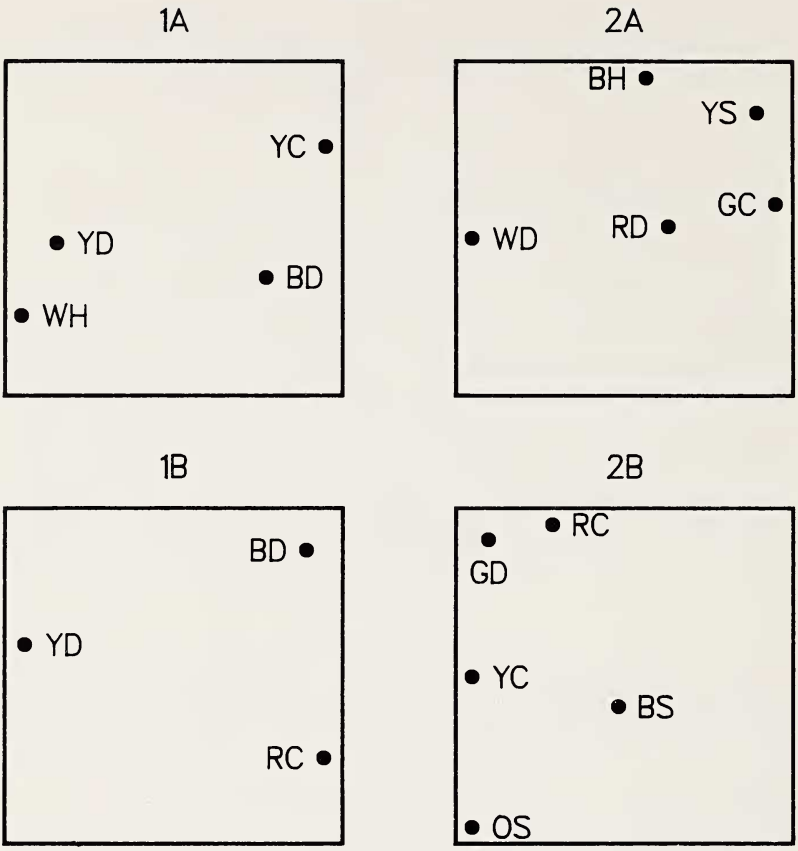

Fig. 1. Spatial relationships of nests placed on floors (each 1m × 1m). Additional nesting tubes were supplied to give a total of 10 on each floor.

apparent from censuses when one or two workers were observed within a tube (cf. Table 2). Sometimes this exploration was followed by immigration, but more often there was no apparent result.

The time scale within which population changes occurred is given in Figure 2. Fighting between workers was most frequent in the first three weeks of the season, and virtually nonexistent after 8 weeks. Similarly, observations of workers carrying other workers were clustered in the first few weeks of the experiments. Exploration of new nesting sites was quite high initially, then fell off by the second

Table 1. Occupants of nests positioned on forest floors in early May

	Marker	Queens	Workers	Eggs	Larvae
Floor 1A	BD	22	91	10	178
	YC	4	30	2	73
	WH	2	24	0	28
	YD	7	80	0	99
Floor 1B	YD	1	20	14	11
	BD	5	13	0	28
	RC	2	28	5	19
Floor 2A	BH	0	13	0	18
	WD	0	9	0	8
	RD	3	9	0	47
	GC	4	63	0	64
	YS	2	39	0	67
Floor 2B	GD	1	12	5	29
	OS	3	11	0	15
	YC	0	101	0	66
	BS	3	29	13	15
	RC	0	21	0	39

week. Moreover, the five observations of tandem running behavior were restricted to the first 2 weeks. Workers and/or brood moved between existing nests primarily within the first four weeks. By mid-June there was little activity on the floors other than routine foraging.

The first month of census data for nests on floor 2B are given in Table 2. From these data we can infer the following: a group of workers moved from RC to GD on May 9. On the 10th, a queen and some workers moved from GD to RC, and the fusion of GD and RC continued over the following three days. On May 28 the YC nest split, with 47 workers moving to GD and 35 remaining behind. At about this time members of the RC site started to explore OH; this tentative exploration continued for about two weeks more. Thus a great deal of information about population fluidity can be gleaned from census data alone.

The census data also showed striking differences in activity between the first few weeks and the rest of the summer. Wholescale migration, fission into subunits, and fusion of nests occurred most often early in the experiments (Figure 3). Of three migration events, two occurred in the first two weeks. Of four fission events, two

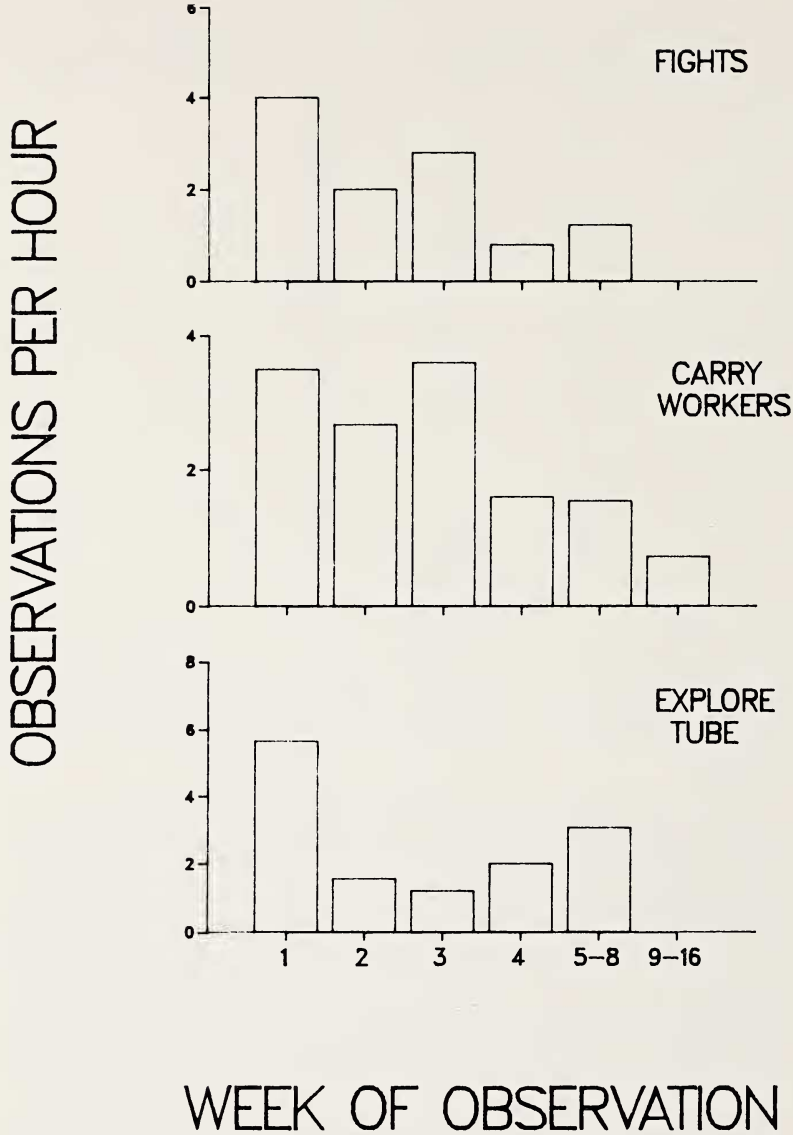

Fig. 2. Frequencies of certain events associated with population changes. The time scale is irregular to indicate how activity dropped off in summer.

occurred in the second week, and one in the fourth week. Of two fusions, one occurred on the third day of observation. The remaining events occurred in late July, and involved ants only on Table 1A (Figure 4): one nest moved and split within the next week; one of those subunits was apparently joined by a second nest immediately thereafter. Thus, although the two nests had not interacted in any discernible way prior to the end of July, they demonstrated a remarkable fluidity after being in place for eight weeks.

Fission rates may be a function of nest size (Stuart 1985). Nests that underwent fractionation tended to have more queens than those which failed to subdivide during this study (average ranks of 10.4 and 8.6, respectively), but this difference was not significant (Mann-Whitney U-test; $P \gg .05$). Similarly, nests that underwent fission tended to have more workers ($\bar{R} = 12.8$) than those which failed to subdivide ($\bar{R} = 7.9$), but again the differences were not significant ($U = 40.6$, $P = .07$). Although the small number of fissions reduced the power of our analysis, nonetheless out results are consistent with Stuart's observations.

Most nests in this experiment reared sexuals. Since it is extremely difficult to mimic the naturally-occurring reproductive flights of this species in the laboratory and thus our observations of reproductive behavior may not be indicative of natural activity, we give only a brief account: males eclosed in late July, and after staying in the nesting tubes for a week or so, they started to emerge onto the forest floor. There they explored and took a few preliminary hops before returning to their natal nests (at which point they were not always allowed reentry). By late August, all males left their nests permanently, and many were dead. Female alates, however, were much more reclusive, and came outside the nest rather infrequently. As a rule, these females were reaccepted into their natal nests readily. In only two cases was a gyne from one nest accepted into a second nest; thus acceptance of non-natal new queens may be rare in nature as well. These observations suggest that polygyny develops in *L. longispinosus* nests primarily when daughters rejoin their nest of origin.

Discussion

Like all laboratory studies, our work can be criticized on the grounds that behavior of disturbed nests in seminatural conditions

Table 2. Census data for nests on Floor 2B. Only ants inside nesting tubes were counted, which produced some variation in worker numbers from day to day.

Site Marker	5/8/84		5/9		5/10		5/11		5/12		5/13		5/14		5/15		5/16	
	Q	W	Q	W	Q	W	Q	W	Q	W	Q	W	Q	W	Q	W	Q	W
GD	1	12	1	25	0	16	0	6	0	1	0	1	0	0	0	0	0	0
OS	3	11	3	9	3	9	3	8	3	9	3	7	3	6	3	7	3	7
YC	0	101	0	95	0	91	0	92	0	94	0	81	0	100	0	95	0	86
BS	3	29	3	26	3	26	3	23	3	16	3	16	3	10	3	15	3	13
RC	0	21	0	7	1	11	1	16	1	24	1	26	1	28	1	19	1	19
OH	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Nest Tube	5/17		5/18		5/21		5/28		6/4	
	Q	W	Q	W	Q	W	Q	W	Q	W
GD	0	1	0	0	0	0	0	47	0	37
OD	3	6	3	6	3	7	3	5	3	2
YC	0	88	0	85	0	76	0	35	0	24
BS	3	12	3	9	3	5	0	3	0	6
RC	1	23	1	19	1	14	1	8	0	4
OH	0	0	0	0	0	0	0	2	1	0

bears no resemblance to field behavior. While sensitive to this argument, we nonetheless maintain that our data can be extended to evolutionary and ecological considerations. There were no gross differences between lab and field behavior; indeed a striking feature of these *Leptothorax* ants is how readily they adapt to laboratory conditions (e.g. Wilson 1975). Comparable studies of polydomy in these tiny ants cannot be conducted in the field. Given that this species adjusts well to captivity and no other avenue of investigation is possible currently, we proceed to interpret results of our laboratory studies.

When the ants were first introduced to the artificial forest floor, they not only encountered a new environment that required exploration, but also met members of other nests. Thus the effects of exploring new habitat and encountering new ants were initially confounded in this study. However, we argue that, within a week, the behavior of these ants came to reflect what might be observed in the field. *Leptothorax* workers seem to become familiar with their surroundings quickly; certainly when these ants are placed into a new nest box the initial intense exploration wanes within 2–3 days. Moreover, the ants would have encountered each other in nature under spring conditions, just as they did in the lab. Therefore, while the effects of exploring a new habitat cannot be separated out, we feel they are relatively inconsequential after the first week of our observations.

The most striking aspect of this study was how critical spring activity is in determining a population structure that remains relatively stable throughout the rest of the summer. The vast majority of aggressive encounters (which may result in intraspecific dulosis (Alloway 1980)), exploration of new nesting sites, apparent recruitment of nestmates (tandem running), and colony subdivision occurred within three weeks of the arrival of "spring". In fact, very little behavior of interest to this study was observed after June 15. Most ants emerging from the nest in summer were apparently searching for food or water; when two individuals met, they usually antennated briefly and then went their separate ways. This pattern is consistent with their natural history. The only field observations of queens walking alone and of workers carrying other workers or brood have been recorded in early May. Extra-nest worker activity from June–August appears restricted to individual foraging (Herbers, pers. obs.).

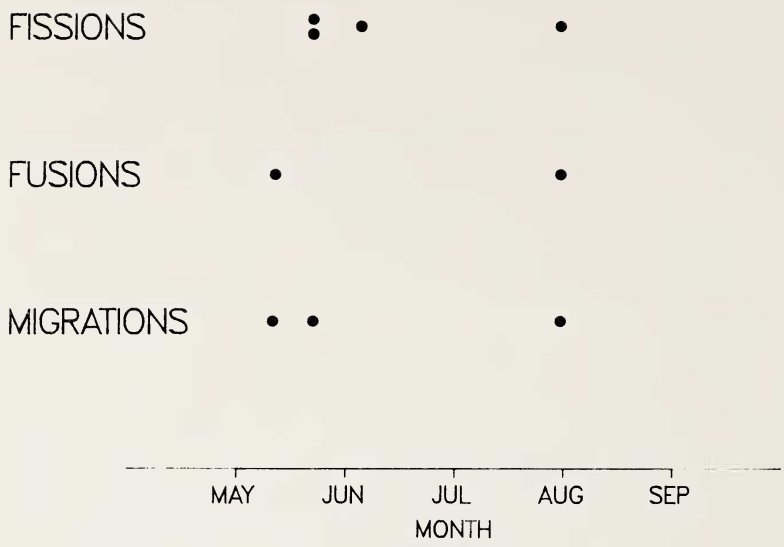

Figure 3. Large-scale events occurred infrequently over the season and were clustered in early spring.

These behavioral observations accord well with inferences made about population structure that are based on spatial distributions of nests and queen distribution among nests (Herbers 1986a). If the cyclic polydomy hypothesis is correct, then the nests used in this study, which had been collected in late fall, had already undergone colony coalition for overwintering. The units that were set out on the floors, then, were presumably functional, independent colonies. When ants from different colonies came back into contact after overwintering, they re-established dominance relations through aggressive encounters and perhaps staked out territories. Likewise, under spring conditions, colonies fractionated to occupy empty nesting sites. After a period of fusions, fissions, brood exchange, and the like, a spatial pattern was achieved that was largely maintained throughout the rest of the summer. We expect that, had we been able to expose the floors to more autumn-like conditions, we would have observed nest fusions and colony condensations to increase.

This seasonal cycle makes comparisons to other studies difficult. Alloway et al (1982) reported that fusion resulted in each of three

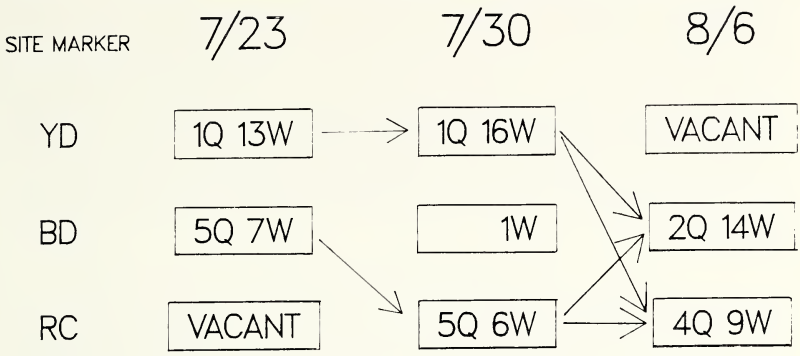

Figure 4. Schema of changes on floor 1A in late July.

separate experiments where 2 nests of *L. longispinosus* were positioned naturally on floors. They also examined the closely related *L. ambiguus,* for which fusions occurred in 16 of 21 replicates. Their experiments were apparently conducted on nests collected from spring through mid-summer, which probably included parts of polydomous colonies. That we observed only 2 fusions in a comparable study may reflect the fact that we placed functional colonies on our floors; a lower fusion rate would be expected for entire colonies than for subunits of polydomous colonies.

In contrast to fusion events, reports of spontaneous polydomy show rough similarity between species. Stuart (1985) found that 12 of 57 nests of *L. curvispinosus* underwent fission in the laboratory, events that were dispersed throughout the season. Our fission rate (4 events for 17 nests) is quite comparable, although we observed spontaneous polydomy primarily in spring. Thus fission events may not be as strongly seasonal as our results imply.

The above data are entirely consistent with the cyclic polydomy hypothesis, since activities associated with colony fractionation (brood transport, tandem running, fissions, worker exchange) occurred mainly in early spring. The fluid nature of this *L. longispinosus* population is quite evident, and can help to explain summer-winter differences in queen and worker distribution (Herbers 1986a). The causes of cyclic polydomy are obscure at present. Colony fission during spring and summer may serve to alleviate competition for food (Herbers 1985), but nest coalition in fall is more

difficult to explain. Condensation for overwintering might serve important social functions. Alternatively, a tantalizing suggestion based on laboratory data is that nest survivorship in winter is a function of resident queen number (Herbers 1986b). If the same relation holds in nature, then nests subunits may have higher survivorship in concert than they would alone. Whatever the proximate and ultimate causes, the seasonal cycle in polydomy deserves closer scrutiny.

Acknowledgments

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